CYTOLOGICAL STUDIES OF DIPLOID AND POLYPLOID FORMS IN RASPBERRIES[1]

By ALBERT E. LONGLEY, *Cytologist, Office of Biophysical Investigations,* and GEORGE M. DARROW, *Pomologist, Office of Horticultural Investigations, Bureau of Plant Industry, United States Department of Agriculture*

This investigation of the raspberries of the subgenus Idaeobatus[2] is a continuation of cytological studies of the pollen-mother-cell development of Rubus begun by the senior author in 1921. In the first investigation, a report of which is now in press, the senior author found that diploid forms, that is, forms with a reduced number of seven bivalent chromosomes, were the exception in the subgenus Eubatus.

The present article presents the result of a careful study of the pollen-mother-cell development of species and varieties used in raspberry breeding by the Office of Horticultural Investigations of the United States Department of Agriculture, in which it is shown that most raspberries have seven bivalent chromosomes.

The study was undertaken to determine the chromosome number of the various species of raspberries as an aid to breeding and especially to find some explanation for the peculiar behavior of hybrids of La France and Ranere (St. Regis) varieties. From 100 or more seedlings of this particular cross only one weak plant gave well-developed fruit. A large percentage (32) bore sterile flowers and the remainder showed a range in fertility from those having an occasional flower in which a drupelet set to those with several drupelets to each flower. La France has been considered a variety of *Rubus idaeus*, the European raspberry, and Ranere, a variety of *R. strigosus*, the American red raspberry. These species are more closely related than many others which, when hybridized, give all, or nearly all, fertile progeny. For example, hybrids of Gregg (*R. occidentalis*) × Ranere (*R. strigosus*) in the same environment as La France × Ranere hybrids are entirely fertile. Certain other forms, when crossed, also gave an unexpectedly large percentage of infertile seedlings. Such results are difficult to interpret and it was hoped that knowledge of chromosome behavior might help to explain them.

The subgenus Eubatus (blackberries) in which the haploid number is seven has many chromosome groups, that is, tetraploid, pentaploid, hexaploid, and octaploid (*12*). The closely related genus Rosa also has the same basic chromosome number seven and has similar chromosome groups (*19*) (*3*) (*14*). Hybrids between polyploidal forms of Rosa are reported to behave in a manner quite different from the simple Mendelian expectation. It was considered possible, therefore, that there were similar polyploidal groups among the raspberries which would explain the results observed. To make the work as systematic, compre-

[1] Received for publication Feb. 9, 1924.
[2] The classification used in this paper is, for the most part, that of Focke given in "Species Ruborum" (*8*).[3]
[3] Reference is made by number italic to "Literature cited," p. 747-748

hensive and helpful as possible, representatives of as many types of raspberries as could be procured were selected with special reference to the economic importance of the groups, their botanical relationship, and their possible value in breeding.

MATERIAL AND METHODS

The plants from which buds were taken were grown at the Bell Horticultural Field Station, Glendale, Md., and at Arlington Experiment Farm, Rosslyn, Va.

Material was collected during the last two weeks of May, in June, and again in September and October (1923). Buds were killed in weak chromo-acetic solution, and in Bouin's killing mixture, both of these being quite satisfactory.

All material was imbedded in nitrocellulose, this medium having been found very satisfactory for this type of investigation. The buds were sectioned about 15 micra thick so as to have uncut nuclei for study.

Heidenhain's haematoxylin was used for staining chromosomes. The mother cells were studied by the use of 2 mm. and 1.6 mm. Zeiss apochromatic lenses and No. 12 and 18 compensation oculars.

Pollen counts were made from anthers that had not dehisced. Plate 1, A, shows a bud in the stage of development usually chosen. The anthers were crushed in water on a glass slide and all plump grains counted as good. As a rule, the count was made from 100 grains only and the percentage of good pollen is, therefore, only approximate. Germination tests and special technique are necessary for a final test.

HISTORICAL AND CYTOLOGICAL DESCRIPTION

For convenience, the classification of Focke has been followed, for the most part, and the results have been presented in sections and series as given in "Species Ruborum" (*8*). The few polyploid forms, however, have been segregated and discussed after the review of the diploid forms.

Brief historical descriptions of many raspberry species and garden varieties are first given. The inconsistency existing in the nomenclature of horticultural raspberry and blackberry forms makes it necessary to include the available history of each species and variety used in this study, since in this way the identity of the material will be established more definitely. These descriptions, which we regret are incomplete, are followed by the results of morphological and cytological studies of pollen and pollen formation.

Table I presents a summary of the pollen counts and the chromosome number and behavior during the pollen tetrad formation of the species and varieties studied. Plates 2 and 3 show drawings of heterotypic prophases selected from type species, varieties, and hybrid forms.

TABLE I.—*Chromosome number and pollen condition of raspberries*

	Percentage of good pollen.	Number of haploid chromosomes.	Behavior of chromosomes at meiosis.	Plate No.
Subgenus Idaeobatus:				
Section Rosaefolii—				
1. *Rubus illicebrosus*	97	7	Regular	
2. *R. thunbergii*	86			
Section Pungentes—				
3. *R. lasiostylus*		7	...do	2 H
4. *R. lasiostylus dizygos*×*R. idaeus* horticultural variety Superlative	40	7	...do	2 K
Section Idaenthi—				
Series Nivei—				
5. *R. coreanus*		7	...do	2 I
6. *R. coreanus*×*R. strigosus* horticultural variety Newman		7	...do	2 L
7. *R. phoenicolasius*		7	...do	2 O
Series Thrysidaei—				
8. *R. adenophorus*		7	...do	2 P
9. *R. innominatus*		7	...do	2 J
10. *R. innominatus*×*R. idaeus* horticultural variety Superlative		7	...do	2 M
11. *R. innominatus*×(*R. idaeus*×*R. strigosus*) horticultural variety Cuthbert [a]	33	7	...do	2 N
Series occidentalis—				
12. *R. occidentalis*—				
Horticultural variety Cumberland		7	...do	2 C
Horticultural variety Farmer		7	...do	
Horticultural variety Gregg	98	7	...do	
13. *R. occidentalis* × *R. idaeus*—				
Horticultural variety Gregg × Wisbeck		7	...do	2 E
Horticultural variety Royal		7	...do	
14. (*R. occidentalis*×*R. idaeus*)×*R. strigosus*—				
Horticultural variety Cardinal	75	7	...do	
Horticultural variety Royal×Newman		7	...do	2 G
15. *R. occidentalis*×*R. strigosus*—				
Horticultural variety Gregg×King [b]	93	7	...do	2 F
Series Eu-Idaea—				
16. *R. mesogaeus*	89	7	...do	2 Q
17. *R. idaeus*—				
Horticultural variety Lloyd George	99	7	...do	2 B
Horticultural variety Magnum Bonum				

[a] The classification of raspberry varieties used is that of Darrow; see literature cited (6).
[b] The pollen count was made from one of the most fertile forms of this cross.

TABLE I.—*Chromosome number and pollen condition of raspberries*—Continued

	Percentage of good pollen.	Number of haploid chromosomes.	Behavior of chromosomes at meiosis.	Plate No.
Subgenus Idaeobatus—Continued.				
Section Idaenthi—Continued.				
Series Eu-Idaea—Continued.				
18. *R. idaeus* (?)—				
Horticultural variety La France	56	14	Irregular...	3 B
Horticultural variety Merveille Rouge	24	14	...do.....	3 E
Horticultural variety Merveille de Quatre Saisons Rouge	28	14	...do.....	3 F
Horticultural variety Surpasse Merveille a blanc	10	14	...do.....	3 G–I
Horticultural variety Souvenir de Desire Bruneau	36	.....	.....	.....
Horticultural variety All Summer	97	21/2	...do.....	.....
Horticultural variety White Queen	96	21/2	...do.....	.....
19. *R. idaeus*×*R. strigosus*—				
Horticultural variety Cuthbert	70	7	Regular...	2 D
Horticultural variety Marlboro	50	.....	.....	.....
20. *R. Idaeus*×*R. strigosus* (?)—				
Horticultural variety La France×Ranere	Variable.	21/2	Irregular...	3 C
Horticultural variety Erskine	50	21/2	...do.....	3 D
21. *R. strigosus*—				
Wild Plant	100	7	Regular...	2 A
Horticultural variety Eaton	.....	7	...do.....	.....
Horticultural variety King	.....	7	...do.....	.....
Horticultural variety Newman	.....	7	...do.....	.....
Horticultural variety Ranere	100	7	...do.....	3 A

DIPLOID RASPBERRIES

SECTION PUNGENTES × IDAENTHI

R. lasiostylus dizygos×*R. idaeus* horticultural variety Superlative. This cross was made by the junior author at the Bell Horticultural Field Station and buds were taken from a selected individual.

SECTION IDAENTHI

R. coreanus×*R. strigosus* horticultural variety Newman. This cross was made by the junior author at the Bell Horticultural Field Station and the buds taken from a selected bush. The *R. coreanus* parent of this hybrid was grown from seed secured from Kew, England, but itself seems to be a hybrid, *R. coreanus*×*R. biflorus*.

R. innominatus S. Moore. The plants of this species were propagated from plants grown by the late Dr. Walter Van Fleet, presumably from seed sent by E. H. Wilson from China.

R. adenophorus Rolfe. The plants of this species were obtained from the Office of Foreign Seed and Plant Introduction, United States Department of Agriculture, under No. 52939.

R. innominatus×*R. idaeus* horticultural variety Superlative. The plant from which buds were taken was one of several of this cross made by the junior author at the Bell Horticultural Field Station.

R. innominatus×(*R. idaeus*×*R. strigosus*) horticultural variety Cuthbert. Horticultural variety Van Fleet. This hybrid was made by the late Doctor Van Fleet at Chico, Calif., and the plants grown from seed at the Bell station.

R. occidentalis. Horticultural variety Cumberland. This was originated by David Miller of Camp Hill, Pa., and introduced in 1898.

Horticultural variety Farmer (Plum Farmer). This was found in a shipment of another variety received by L. J. Farmer, Pulaski, N. Y., and introduced by him in 1895. Farmer, as an early sort, and Cumberland as a late variety are the leading black raspberries grown in the United States.

R. occidentalis×*R. idaeus*. Horticultural variety Gregg×Wisbeck. The buds were collected from one of several seedlings of this cross made by the junior author at the Bell station.

Horticultural variety Royal. This variety was originated in Indiana by L. H. Gerton, and was introduced by L. J. Farmer, Pulaski, N. Y., in 1909.

(*R. occidentalis*×*R. idaeus*)×*strigosus*. Horticultural variety Cardinal. This variety originated on the place of A. H. Griesa, Lawrence, Kans., in 1888, apparently from seed of the Shaffer. Because of its glandular hairy inflorescence it is considered a cross of the Shaffer with a variety of *R. strigosus* (*4*).

Horticultural variety Royal×Newman. The material for study was taken from a plant growing at the Bell station which was one among the many crosses of this parentage made by the junior author.

R. occidentalis×*R. strigosus*. Horticultural variety Gregg×King. This material for study was taken from one plant, which was selected for its good fruit, from a large number of plants of this cross made by the junior author, at the Bell station. Most seedlings of this cross were partly sterile, setting but few drupelets to each flower. This seedling was selected as the best and its pollen count showed a notably high percentage of good pollen grains. The seed parent was a variety of black raspberry resembling Gregg but concerning the identity of which there was some question. The abundant glandular inflorescence clearly distinguishes these crosses from the Royal and the Gregg×Wisbeck.

R. idaeus. Horticultural variety Lloyd George. This variety was found wild and introduced by J. H. Kettle, Corfe Mullen, Winborne, Dorsett, England, in 1920.

Horticultural variety Magnum Bonum. This old variety of Europe was introduced into America about 1840. It differs markedly from the other European raspberries which we have studied. The turions are densely covered with glandular bristles and it resembles mountain and maritime forms.

R. idaeus×*R. strigosus*. Horticultural variety Cuthbert. This variety originated as a chance seedling in the garden of Thomas Cuthbert at Riverdale, N. Y., about 1865 growing near plants of the Hudson River Antwerp, a variety of *R. idaeus*. It is, therefore, considered a hybrid of *R. idaeus*×*R. strigosus*.

Horticultural variety Marlboro (*Abundance, Laxton's Abundance, Perfection of England*). The material used was gathered from plants received as Laxton's Abundance from Laxton Bros., England, a variety which was determined to be identical with Marlboro by Grubb (*9*). This is confirmed by our examination. Marlboro was originated by A. J. Caywood, Marlboro, N. Y., as a cross of Highland Hardy, and a seedling from English Globe and the Hudson River Antwerp (*5*), and introduced in 1884. Highland Hardy is supposed to be a variety of *R. strigosus*. November Abundance is probably a distinct sort, having originated in England.

R. strigosus Mchx. Wild plants from Hebron, N. Y. In September, 1920, selections were made of bushes fruiting freely in the fall on turion tips. These were transplanted to the collection of the Bell Horticultural Field Station.

Horticultural variety Eaton. Found as a chance seedling at Cambridge City, Ind., in 1885. Its glandular inflorescence refers it to *R. strigosus*.

Horticultural variety King. The history of this variety is not entirely clear. It is widely grown in the upper Mississippi Valley States. The buds used were from plants of this variety secured from Michigan. It is supposed to be the Thompson's King sent out by the Cleveland Nursery Co. of Rio Vista, Va., in 1892, which variety was grown from seed of Thompson by T. Thompson of Richmond. Beach, in 1895, however, states of this variety, "Canes vigorous, show evidence of *Idaeus* parentage" (*2, p. 204*). King, as grown to-day, does not show evidence of *R. idaeus* parentage, except perhaps in that a large percentage of its progeny are more or less infertile, but it has the glandular inflorescence, the thin leaves, and light-red fruit of *R. strigosus* and is very hardy. Over 100 hybrids with a black raspberry and many hundred other hybrids and crosses with it made by the junior author fail to show characteristics of *R. idaeus* but do show characteristics of *R. strigosus* and it is classified accordingly.

Horticultural variety Newman. This variety was grown from seed of Eaton, by C. P. Newman, La Salle, Quebec, and was introduced by the Provincial Government of Quebec, Canada, in 1921. Its hardiness and light red fruit refer it to this species. Newman states that the pollen parent may have been King.

Horticultural variety Ranere (*St. Regis*). The Ranere was found wild near Hammonton, N. J., by A. Ranere and was extensively grown by him and others several years before 1910 when it was introduced under the name "St. Regis." It is densely glandular, hairy, very hardy, has thin leaves and light red fruit, and is referred to *R. strigosus* (*6*).

Table I shows that all raspberries examined cytologically can be separated into two classes, those with seven haploid chromosomes, and those with more than seven.

Such a division also separates all species into two groups based on the distribution of the chromosomes during the reduction divisions of the pollen mother cell. The diploid species, that is, those showing seven bivalent or haploid chromosomes just previous to the first reduction division, have the somatic or univalent chromosomes pairing very promptly in the prophase of the first reduction division, and these bivalent chromosomes divide regularly and promptly in both the first and second divisions. Such a division gives a quantitatively equal distribution of all chromatin material to the four daughter nuclei, and consequently this type of division has been termed regular. However, a study of the reduction phases showed, in rare cases, a little tardiness in pairing of univalent chromosomes, or occasionally a single chromosome lagging behind its associates in reaching the pole after either the first or the second reduction division but these irregularities were so rare that they may be disregarded.

POLYPLOID RASPBERRIES

The following section is a discussion of a smaller group of horticultural varieties of raspberries in which the chromosome number is larger than is the rule in diploid forms and in which chromosomes show characteristic irregularities in their distribution during meiosis.

R. idaeus (?). Horticultural variety La France. This variety was secured from the introducer, John Scheepers Co., New York City. The original stock was introduced from France probably between 1890 and 1900 and grown at Stamford, Conn., from which place it was distributed. It resembles Merveille de Quatre Saisons Rouge very closely and may be identical with it.

Horticultural variety Merveille Rouge. This old French variety was raised and introduced by Simon Louis Frères of Metz, France. Our stock which was secured from Laxton Bros., Bedford, England, is very similar to Merveille de Quatre Saisons Rouge.

Horticultural variety Merveille de Quatre Saisons Rouge. This is probably the same as Perpetual de Billiard. It was raised and introduced in 1849 by M. Billiard, nurseryman of Fontenay, near Paris. Stock of this was obtained from Orleans, France. It is one of the old varieties and is reported as identical with October Red (*20*) and the Old Double-Bearing (*18*). It is also reported as a supposed seedling of Fastolff (*16*).

Horticultural variety Surpasse Merveille a Blanc. Stock under this name was secured from Orleans, France, but it bears red fruit and resembles Merveille de Quatre Saisons Rouge very closely and its probable identity with this variety is indicated further by this cytological study.

Horticultural variety All Summer. Plants of this variety were obtained from Orleans, France.

Horticultural variety White Queen. White Queen was introduced in 1920 by Wm. M. Hunt & Co., of New York City, who state that it may be of French parentage. It was found on the place of Jonathan Thorne at Black Rock, Conn., and is supposed to be a chance seedling. It fruits freely in the autumn on young canes.

La France was the first raspberry studied in which more than the 7 haploid chromosomes were found and, because of this, all phases of meiosis have been studied critically. Plate 3, B, pictures the 14 bivalent chromosomes. They appear crowded in the drawing, but are on the periphery of the nucleus and quite separate in the actual observations. Not only is there an increase in chromosome number above that of diploid forms, but there is also a change in the general appearance of the anthers. Clear figures, plump mother cells and prompt pairing of the chromosomes at diakinesis are absent and one has to study much material and stain carefully in order to overcome the unfavorable conditions found in this polyploid form during meiosis.

It seems unnecessary to discuss in detail the reduction divisions of this variety but one characteristic should be mentioned, that is, the irregular distribution of chromosomes, some of which lag on the spindle and are extruded from the daughter nuclei. Such behavior is believed to indicate hybrid origin, and results in the formation of pollen grains with varying chromosome numbers and varying in viability.

La France, though not hardy, endures the winters better than many European raspberry varieties. It has dark green foliage which is more resistant to leaf spot than spring fruiting European sorts. It also bears fruit quite freely on the turion tips in the autumn. Five varieties with characteristics similar to La France were selected and five additional polyploidous forms were found. The cytological study of these forms had associated with it the difficulties referred to in the foregoing variety. The mother cells frequently were thin and vacuolated and collapsed before they reached the tetrad stage. After much search favorable figures of many stages were found.

The 14 haploid chromosomes of Merveille Rouge and Merveille de Quatre Saisons Rouge are represented in Plate 3, E and F. These typical prophases resemble that pictured for La France and the later phases have associated with them the same interesting irregularities. Consequently, one would expect to find a large amount of pollen sterility, an expectation borne out by the actual observations, both varieties having only 25 per cent viable pollen.

Surpasse Merveille a Blanc has 14 bivalent chromosomes. The early prophases which showed the univalents grouped in pairs were very favorable for study. Plate 3, G was drawn from a figure that had only three bivalent chromosomes, the remaining 22 univalents are seen grouped in pairs. A later prophase showing only bivalent chromosomes is represented in Plate 3, H. Plate 3, I, is a drawing of a very late heterotypic

prophase or early metaphase. Seven chromosomes are at the equatorial plate, some even having divided, while the remaining 7 are lagging in their approach to the plate. It is these laggards that cause observed irregularities in this and the homotypic division. They are again tardy in their movement from the nuclear plate and may not be included in the daughter nuclei and so the resulting pollen grains do not receive either a qualitatively or quantitatively equal amount of chromatin material. This type of reduction is styled as irregular.

The chromosome number of varieties White Queen and All Summer seems to be $\frac{21}{2}$. During meiosis they show many of the irregularities peculiar to triploid hybrids, and, consequently, they are grouped with the foregoing polyploidous raspberries. The pollen of these two sorts, however, seems remarkably good when their chromosome condition is considered.

R. strigosus × *R. idaeus*, (?). Horticultural variety Erskine. This originated at Lee, Mass., with E. J. Norman, being found in 1895 among Marlboro plants set in 1890. Two other varieties, the Cuthbert and Golden Queen, were being grown by Norman at that time. As the plant was small, he supposed it to be a seedling of the Marlboro. The Marlboro plants were obtained from Ellwanger & Barry of Rochester, N. Y., who also were growing Fontenay and other European raspberries. Fontenay is an autumn-fruiting sort and probably belongs to this polyploid group. There is a bare possibility that Erskine may have come from that source. If the assumption that Erskine originated from the Marlboro is correct then it is the only polyploid variety of American origin derived from American varieties yet found.

Horticultural variety La France × Ranere. These hybrids were made by the junior author at the Bell Horticultural Field Station and two of the seedlings, one entirely sterile, the other nearly so, were selected for this study.

Erskine was the second polyploid raspberry discovered and difficulty was experienced in finding good mitotic figures to study the various phases of this form. This supposed hybrid is triploid, and the reduced chromosome number is represented in Plate 3, D. There are generally 10 chromosomes at diakinesis. In the earlier study of the Eubatus subgenus by the senior author, triploid forms were found to be very abundant, and this hybrid behaves in a manner very similar to that described for triploid blackberries. Seven of the bivalent chromosomes behave in a regular manner during the reduction phases, but the remaining chromosomes are slow about fusing in the heterotypic prophase. These laggards are distributed, during meiosis, in an irregular manner to the four daughter nuclei or are frequently extruded into the cytoplasm where they degenerate or become the nuclei for dwarf pollen grains.

The hybrid, La France × Ranere, is triploid, which would be the natural result if the parents contributed 14 and 7 chromosomes, respectively. Plate 3, A, B, and C, represents prophases of the parents and the hybrid. This opportunity to study an F_1 raspberry hybrid has shown that it behaves in a manner very similar to that described by Rosenberg (*15*) for the well-known Drosera hybrid. This artificially produced raspberry hybrid has all the irregularities of chromosome distribution noticed in triploid blackberries, and furnishes additional evidence that many of our blackberries are very recent hybrids.

In collecting material of this La France × Ranere cross, buds were gathered from two seedlings, No. 1 and No. 2. All anthers of No. 1, as pictured in Plate 1, C, were so sterile that it was impossible to find normal reduction phases. Such extreme sterility recalls the sterility of *Prunus cerasus* × *P. avium* as reported by Dutrochet (7) who writes, "The 'stamina'

formed a compact mass in which no pollen was formed." Form No. 2 was more fertile, as the anthers pictured in Plate 1, B, show. From this plant there was procured sufficient material for a study of the reduction division. Since this hybrid is triploid, it corresponds to the intergroup crosses of wheat (Triticum) in which Sax (*17*) found the greatest sterility. It indicates that the sex cell on La France side had 14 chromosomes. The behavior in egg formation, therefore, differs from that studied by Täckholm for the Canina group of roses. He found that the viable egg of a tetraploid species had 21 chromosomes and the viable pollen usually had 7 chromosomes.

It seems certain that this list of polyploid raspberries is not complete. The varieties Buckeye, Hailsham, and Souvenir de Desire Bruneau show external characteristics which place them in this group, that is, as grown in the United States, they are more hardy than the diploid varieties of *R. idaeus*, have heavy dark green foliage, resist leaf spot, and bear fruit on young canes in autumn.

DISCUSSION

POLLEN STERILITY IN RASPBERRIES

Table I shows a dozen diploid forms in which the per cent of good pollen has been determined. Five of these diploid varieties are hybrids, and the large amount of sterile pollen existing in them, in contrast to the small amount of sterile pollen that generally exists in stable species, supports the view that hybridizing may cause noticeable sterility in the offspring (*10*).

This table also shows a second group of sterile raspberries, including all but two of the polyploidous forms. The high percentage of good pollen found in the two exceptions was unexpected, and since a study of these varieties is not complete, no explanation will be attempted. The remaining six forms are very sterile and characterized by an unequal distribution of the chromosomes during the pollen tetrad formation. This extreme sterility may be attributed to unbalanced chromosome conditions existing in the nucleus of the pollen grain, which in turn is recognized as a character of hybrids between incompatible species. The inference, therefore, seems to be that raspberries showing pollen sterility are of hybrid origin and that polyploidous raspberries are the result of crosses between plants belonging to different chromosome groups.

CHROMOSOME MULTIPLICATION DUE TO HYBRIDIZATION

Polyploidy in raspberries seems to have originated in both Europe and America. Our knowledge is too limited to allow the acceptance of one explanation to the exclusion of all others as to how it originated, but the present data support the theory that polyploidism in raspberries has originated through hybridization.

In England *Rubus caesius*, a tetraploid trailing blackberry, blossoms at approximately the same season as the raspberries, while the common blackberries blossom several weeks later than the usual raspberry flowering season. A species with dark thick leaves, similar to *R. caesius*, seems essential to explain the characters present in polyploid raspberries. One English autumn-bearing raspberry was reported as a hybrid, *R. caesius* × *R. idaeus* (*11*). The junior author has raised many *R. idaeus* ×

R. caesius crosses from seed and obtained a great variety of forms, but unfortunately these F_1 plants had been destroyed previous to this study and no cytological material is available.

An F_3 hybrid, originated by Professor Ness (*13*) of the Texas Experiment Station, is a cross between the Cardinal raspberry, a diploid form, and *R. rubrisetus*, a southern blackberry. A cytological study of this hybrid seems to provide evidence to support the theory of the origin of polyploidism in raspberries through hybridization and selection.

Three figures drawn from early reduction phases of this F_3 hybrid show the cytological conditions in this hybrid. Plate 3, J and K, shows the 14 chromosomes of this tetraploid form, while Plate 3, L, pictures a slight irregularity in chromosome distribution. It was exceptional to find irregularities during meiosis, but the history of this hybrid shows that it has been selected through several generations and now behaves like a stable species.

This F_3 hybrid demonstrates that fertile raspberry-blackberry hybrids are possible and it also shows that a tetraploid Rubus has been experimentally produced with the characteristics of a stable species.

After studying many known raspberry × raspberry hybrids without finding a single case of chromosome multiplication it seems worth while to consider the possibility that all the polyploidous forms described in this article are the result of raspberry × blackberry hybrids that have been selected artificially or naturally and now have found a place in our commercial varieties of raspberries.

SIGNIFICANCE OF DIPLOID, TRIPLOID, AND TETRAPLOID RASPBERRIES

We have shown that all the species or varieties of raspberries examined have the basic chromosome number seven. Furthermore, hybrids even between species which are quite different in their external characters also have the same basic number seven. A few varieties referred to *R. idaeus*, however, are triploid or tetraploid and the presence of these few variant forms, in a group otherwise uniform in this respect, is important.

There are genera in which chromosome multiplication has been reported, and in which new hybrid species and varieties are appearing continually. The blackberries, roses, and hawthorns are well known examples where multiplication of species and varieties is associated with chromosome multiplication. In Europe several thousand Eubatus Rubi have been collected and described as species while the recent American publication on "Standardized Plant Names" (*1*), devotes 50 pages to listing varieties of roses alone. The presence of a few polyploid raspberries, of unquestionably recent origin, may be the beginning of a similar multiplication in raspberry forms. All polyploidous raspberries belong to the best autumn-fruiting European group, and, therefore, an effort should be made to combine by hybridization their good qualities with those of our hardy American varieties.

La France × Ranere hybrids, obtained at the Bell station by the junior author demonstrate the variable results that may be expected from intergroup hybrids. The raspberry breeder who attempts to introduce the characters present in polyploid raspberries by hybridization will find his efforts seriously limited by the incompatibility frequently existing between hybrids involving different chromosome groups.

The recent study of tetraploid Datura hybrids (*4*) is a carefully planned scientific research into the genetic behavior of a recently discovered

group of polyploid forms. This pioneer investigation shows that the chances of obtaining new combinations have increased with an increase in chromosome number and it has been found by studying large populations from such hybrids that the offspring follow certain genetic laws of segregation. It is only by means of such experimental hybridization that the plant breeder, who is working with a genus such as Rubus, may help to deduce laws of inheritance that will aid him to combine desirable qualities from the varied material at hand and segregate them in the later generations.

SUMMARY

Diploid species and hybrids are the rule in the Idaeobatis subgenus of Rubus.

Triploid and tetraploid forms are few in number but are a significant and characteristic group of raspberries.

This study suggests that polyploid raspberries are *Idaeobatis* × *Eubatus* hybrids.

Polyploidism, if once established in a group, is likely to increase; consequently the breeder attempting interchromosome group crossing will find his difficulties increased, the interpretation of results more difficult, but the chance of obtaining new combinations of characters multiplied.

LITERATURE CITED

(1) AMERICAN JOINT COMMITTEE ON HORTICULTURAL NOMENCLATURE.
1923. STANDARDIZED PLANT NAMES. Prepared by F. L. Olmsted, F. V. Coville and H. P. Kelsey. 546 p. Salem, Mass.

(2) [BEACH, S. A.]
1895. RASPBERRIES. *In* N. Y. State Agr. Exp. Sta. Bul. 91, p. 201–207.

(3) BLACKBURN, K. A., and HARRISON, J. W.
1921. THE STATUS OF THE BRITISH ROSE FORMS AS DETERMINED BY THEIR CYTOLOGICAL BEHAVIOR. *In* Ann. Bot., v. 35, p. 159–188, 5 fig., pl. 9–10. Literature cited, p. 186–187.

(4) BLAKESLEE, A. F., BELLING, John, and FARNHAM, M. E.
1923. INHERITANCE IN TETRAPLOID DATURA. *In* Bot. Gaz., v. 76, p. 329–374. Literature cited, p. 372–373.

(5) CARD, F. W.
1917. BUSH-FRUITS. New rev. ed., 409 p., illus. New York.

(6) DARROW, G. M.
1920. ARE OUR RASPBERRIES DERIVED FROM AMERICAN OR EUROPEAN SPECIES? *In* Jour. Heredity, v. 11, p. 178–184, illus.

(7) DUTROCHET, M.
1832. STERILITY OF HYBRID PLANTS. *In* Gard. Mag. [London], v. 8, p. 500.

(8) FOCKE, W. O.
1910–14. SPECIES RUBORUM. 3 v., illus. Stuttgart.

(9) GRUBB, N. H.
1922. COMMERCIAL RASPBERRIES AND THEIR CLASSIFICATION. *In* Jour. Pomol. and Hort. Sci., v. 3, p. 11–35, illus.

(10) HOAR, C. S.
1916. STERILITY AS THE RESULT OF HYBRIDIZATION AND THE CONDITION OF POLLEN IN RUBUS. *In* Bot. Gaz., v. 62, p. 370–388, pl. 10–12. Literature cited, p. 386–387.

(11) LAXTON, T.
1874. AUTUMN-BEARING RASPBERRY. *In* Gard. Chron., v. 2, p. 466.

(12) LONGLEY, A. E.
1923. CYTOLOGICAL STUDIES IN THE GENERA RUBUS AND CRATAEGUS. *In* Amer. Nat., v. 57, p. 568–569.

(13) NESS, H.
1921. BREEDING WORK WITH BLACKBERRIES AND RASPBERRIES. *In* Jour. Heredity, v. 12, p. 449–455, illus.

(14) PENLAND, C. W. T.
1923. CYTOLOGICAL BEHAVIOR IN ROSA. *In* Bot. Gaz., v. 76, p. 403–410, pl. 21–22. Literature cited, p. 409.
(15) ROSENBERG, O.
1909. CYTOLOGISCHE UND MORPHOLOGISCHE STUDIEN AN DROSERA LONGIFOLIA × ROTUNDIFOLIA. K. Svenska Vetensk. Akad. Handl., Bd. 43, no. 11, 65 p., 33 fig., 4 pl. Litteraturverzeichnis, p. 61–62.
(16) RIVERS, Thomas
1863. SEEDLING FRUITS—RASPBERRIES. *In* Gard. Chron., 1863, p. 244–245.
(17) SAX, Karl
1923. THE RELATION BETWEEN CHROMOSOME NUMBER, MORPHOLOGICAL CHARACTERS AND RUST RESISTANCE IN SEGREGATES OF PARTIALLY STERILE WHEAT HYBRIDS. *In* Genetics, v. 8, p. 301–321, illus. Literature cited, p. 320–321.
(18) SCOTT, F.
1875. THE AUTUMN-BEARING RASPBERRY. *In* Gard. Chron., v. 4, p. 721.
(19) TÄCKHOLM, G.
1923. ZYTOLOGISCHE STUDIEN ÜBER DIE GATTUNG ROSA. *In* Acta. Horti Bergiani, t. 7, p. 97–381, 56 fig. Litteraturverzeichnis, p. 376–381.
(20) TILLERY, Wm.
1875. THE AUTUMN-BEARING RASPBERRY. *In* Gard. Chron., v. 4, p. 721.

PLATE 1[a]

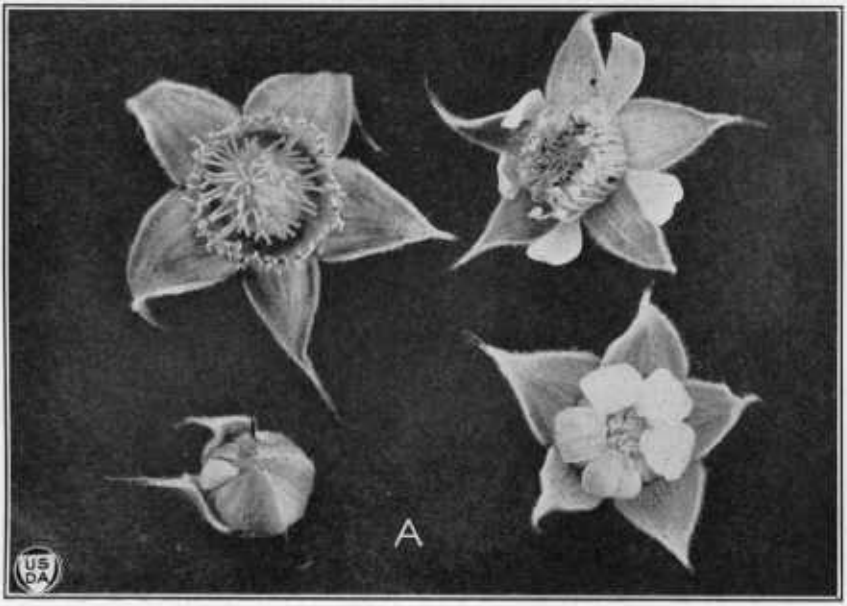
A.—Red raspberry buds and flowers. Pollen counts were made, for the most part, from anthers taken from buds at approximately the stage of development shown in the youngest bud.

B.—Photomicrograph of an anther from a La France×Ranere hybrid that was used for the study of the chromosome behavior in this triploid individual.

C.—Photomicrograph of anther from a sterile La Franc×Ranere hybrid.

---

[a] The drawings of Plates 2 and 3 were made with a 2mm. Zeiss apochromatic lens, a No. 18 compensation ocular and a camera lucida. One exception, Plate 3, G, was made with a 1.7 lens and a No. 12 ocular. All drawings were made with the paper on the table level with the base of the microscope.


A


B


C

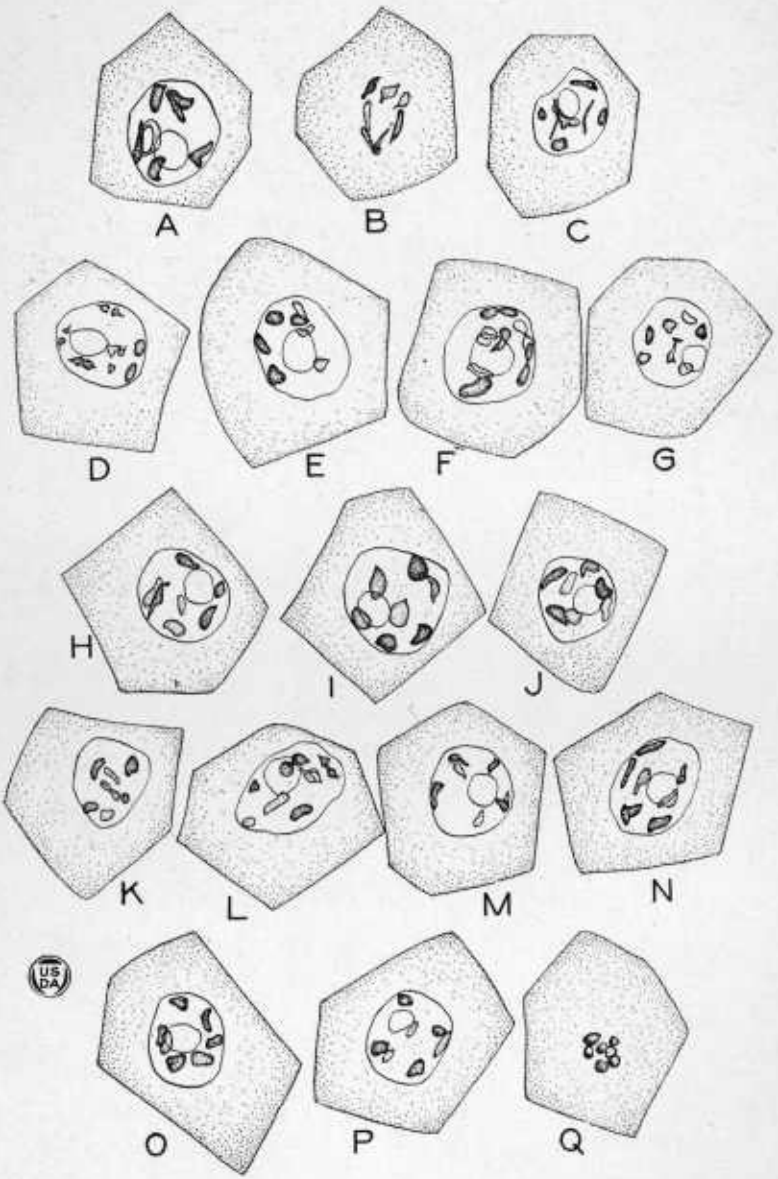

A
B
C
D
E
F
G
H
I
J
K
L
M
N
O
P
Q

PLATE 2

Pollen-mother-cells of rubi at diakenisis:[a]

A.—*Rubus strigosus.*
B.—*Rubus idaeus.* Horticultural variety Lloyd George (early heteroptypic metaphase).
C.—*Rubus occidentalis.* Horticultural variety Cumberland, showing the two, long, slender chromosomes.
D.—*Rubus idaeus*×*strigosus.* Horticultural variety Cuthbert (early prophase).
E.—*Rubus occidentalis*×*idaeus.* Horticultural variety Gregg×Wisbeck.
F.—*Rubus occidentalis*×*strigosus.* Horticultural variety Gregg×King.
G.—*Rubus* (*occidentalis*×*idaeus*)×*strigosus.* Horticultural variety Royal×Newman No. 23.
H.—*Rubus lasiostylus.*
I.—*Rubus coreanus.*
J.—*Rubus innominatus.*
K.—*Rubus lasiostylus* variety *dizygos*×*idaeus* horticultural variety Superlative.
L.—*Rubus coreanus*×*strigosus* horticultural variety Newman.
M.—*Rubus innominatus*×*idaeus* horticultural variety Superlative.
N.—*Rubus innominatus*×(*idaeus*×*strigosus*) horticultural variety Cuthbert.
O.—*Rubus phoenicolasius.*
P.—*Rubus adenophorus.*
Q.—*Rubus mesogaeus.*

---

[a] Drawings reduced one-half.

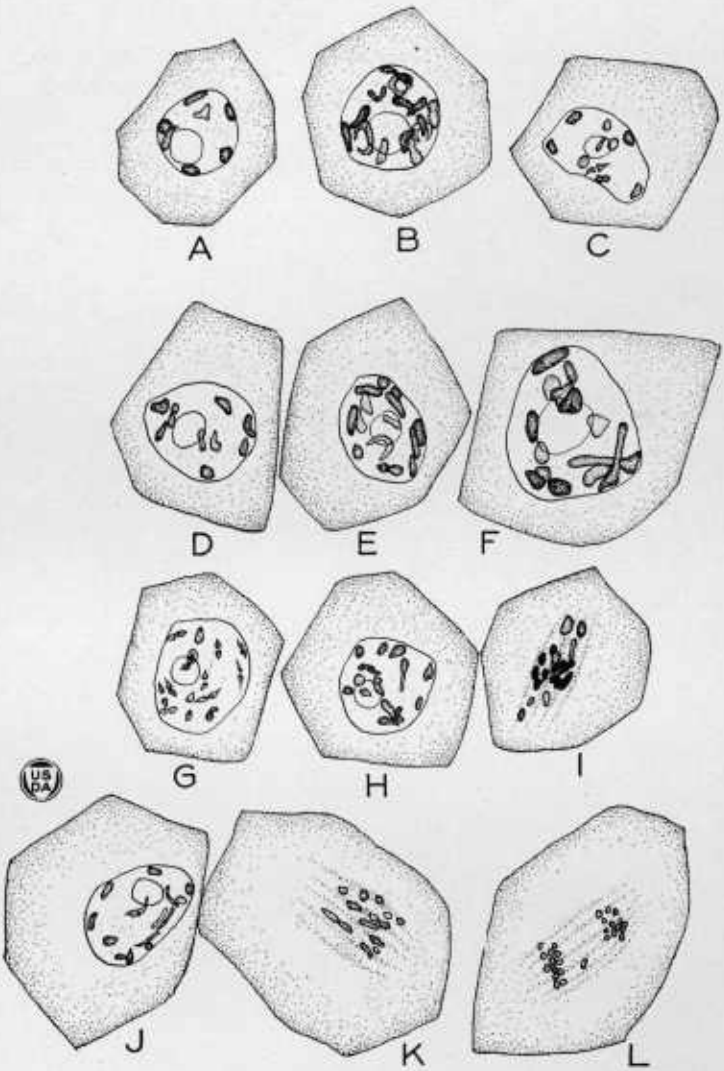
PLATE 3

Pollen-mother-cells of some polyploidous rubi:[a]

A.—*Rubus strigosus*. Horticultural variety Ranere, diploid.
B.—*Rubus idaeus* (?). Horticultural variety La France, tetraploid.
C.—*Rubus idaeus* (?)×*strigosus*. Horticultural variety La France×Ranere, triploid.
D.—*Rubus strigosus*×*idaeus*, (?). Horticultural variety Erskine, triploid.
E.—A tetraploid Rubus, Merveille de Rouge.
F.—A tetraploid Rubus, Merveille de Quatre Saisons Rouge.
G, H and I.—Three stages in the heterotypic division of Surpasse Merveille a blanc.
J, K and L.—Three stages in the heterotypic division of the Ness, a tetraploid raspberry-blackberry hybrid.

---

[a] Drawings reduced one-half.


A
B
C
D
E
F
G
H
I
J
K
L